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Effect of Photoperiod on Body Mass, and Daily Energy Intake and Energy Expenditure in Young Rats

POLLY BOON,*[1] HENK VISSER*† AND SERGE DAAN*

*Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands, and †Center for Isotope Research, University of Groningen, Nijenborgh 4, 9747 AG Groningen, The Netherlands

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BOON, P., H. VISSER, AND S. DAAN. *Effect of photoperiod on body mass, and daily energy intake and energy expenditure in young rats.* PHYSIOL BEHAV **62**(4) 913–919, 1997.—In this experiment we investigate the effect of photoperiod on locomotor activity, body mass, food intake, growth efficiency (relationship between body mass change and food intake), energy expenditure, and body composition in growing Wistar rats. Two groups of animals were subjected to either a long, LD 18:6 (n = 8), or short photoperiod, LD 6:18 (n = 7), during a period of 190 days after weaning. Activity, body mass, food intake, and energy expenditure were measured during the study, as well as body composition at the end of the experiment. We show that growing rats exposed to short photoperiods (a) have a lower rate of weight gain, (b) have similar energy intakes, (c) have lower growth efficiency, (d) have lower daily energy expenditure and resting metabolic rate, and (e) gain less lean body mass than those exposed to long photoperiods. We suggest that the distribution of energy expenditure and food intake over the total 24-h cycle may be responsible for the differences in body weight gain between the two photoperiods. © 1997 Elsevier Science Inc.

Growth Photoperiod Body mass Food intake Energy expenditure Rats

MANY species of mammals undergo pronounced seasonal fluctuations in body mass, although the direction of these fluctuations varies (14,33). Such fluctuations in adult mammals have been shown to be under the control of day length. Voles, for example, reduce their body mass when subjected to short photoperiods, whereas Syrian hamsters are known to increase their body mass under these circumstances (5,6,8,33). Also the growth rates of juveniles are influenced by day length (21,22,24,32). Growing male collared lemmings exposed to short photoperiods (LD 8:16) at weaning show a higher increase in body mass than animals subjected to a long photoperiod (LD 20:4) (21). The response of body mass on photoperiod in both adult and juvenile animals is a seasonal adaptation to a changing environment, which has major consequences for survival rate and future reproduction (5,16).

Obese Zucker rats, when exposed to a long photoperiod (LD 14:10) for 9 weeks (from 1 week after weaning), increase their body mass more than rats from a short photoperiod (LD 10:14), without showing differences in food intake (17). It was hypothesized (17) that a possible factor contributing to the observed effect is a difference in activity level between the two photoperiods. By reducing the active (nocturnal) phase, the animals presumably reduce their daily energy expenditure and spend more time resting. Another possible explanation given is a change in metabolic efficiency (17). Rats take their meals mainly during the dark period. Consuming the same amount of energy in a shorter time period could have a positive effect on the feeding efficiency and could therefore result in a larger increase in body mass per gram of food intake (17). In contrast no effect of photoperiod on growth in lean rats was observed (17), which could be due to the minor difference in day length (4 h) between the two photoperiods.

Body weight gain is the resultant of daily rates of energy intake and energy expenditure. It is not known for any of the species studied so far whether day length generates differences in weight gain increase by affecting energy intake and/or energy expenditure. Our study addresses this question. We studied the rate of weight gain of rats exposed to different day lengths. Rats were chosen because their weight gain responds to other manipulations of the light–dark cycle (18,27,31), although responses to day length appear to be restricted to weight gain in obese Zucker rats (17). We exposed nonobese male Wistar rats to two different photoperiods which differed in day length by 12 h and examined the effect of photoperiod on locomotor activity, body mass, growth efficiency, food intake, energy expenditure, and body composition. We extended the experiment until 190 days after weaning to examine the effect of photoperiod on adult body mass and composition.

[1] To whom requests for reprints should be addressed. E-mail: P.Boon@biol.rug.nl

METHODS

Animals and Housing

Male Wistar rats were randomly assigned to either a long, LD 18:6 (n = 8), or short photoperiod, LD 6:18 (n = 7) (lights on at 2130 or 0930 hours (MET), respectively) directly after weaning, when the animals were 4 weeks of age (=Day 0). The animals were housed individually in perspex cages ($l \times b \times h$: 25.5 × 25.5 × 30 cm^3) with wood shavings for bedding. The cages were placed in two different light-tight wooden boxes (each with its own photoperiod). The boxes were placed in a dark, sound-attenuated room at 25°C and 65% humidity. Every 2–4 days, the animals were weighed at the end of the light episode, and food intake was recorded at the same time. At four time points during the experiment (at Days 15, 30, 90, and 160), the distribution of food intake over the light and dark episodes was recorded by weighing the feeder at the start and end of the different episodes.

Food (RMH-B, Hope Farms BV, The Netherlands), a pelleted diet containing 22.8% (w/w) crude protein and 17.7 $kJ \cdot g^{-1}$, and water were freely available. To obtain an expression for the "efficiency" in which food increases body mass, we calculated the change in body mass over 2–4 days and divided this by the amount of food (g) eaten over the same period: the growth efficiency.

Locomotor activity was continuously recorded by passive infrared detectors (PID, Wonderex FX-35) placed above the home cages of seven animals of each group. Movements detected were automatically recorded every 2 min throughout the experiment. For the calculation of the total activity over 24 h and the activity during the light and dark episodes, the 2-min values were added for the different episodes. To calculate the intensity of activity during the light and dark episodes, the total amount of activity per episode was divided by the amount of hours in each episode.

Energy Expenditure

We measured daily energy expenditure (DEE) at regular time intervals with indirect calorimetry, in which oxygen consumption and carbon dioxide production are measured in an open air flow system. For this, the animals were removed from their home cages and placed in airtight metabolic boxes of 20 L with wooden shavings for bedding. The boxes were placed in light- and temperature-regulated metabolic chambers. The light schedule and temperature were identical to the conditions in the home cages. The animals were placed in the metabolic boxes during the light period. Metabolism was measured over a period of at least 25 h to obtain a full 24-h record after possible handling and gas equilibration effects had subsided. During the measurement food and water were freely available. Body mass was recorded at the start and end of the measurement.

Dry air was pumped through the boxes at rates varying with age (from ca. 45 $L \cdot h^{-1}$ on Day 8 to ca. 120 $L \cdot h^{-1}$ on Day 152) to obtain a difference in % oxygen in the in- and outflowing air of about 0.5%. The flow rate was measured on the inlet air with a mass-flow controller (Type 5850E, Brooks) to an accuracy of 1%. The excurrent air was dried over molecular sieves (3 Å, Merck). The oxygen concentration in the in- and outflowing air was measured by a zirconium oxide sensor (S-3A/II Oxygen Analyzer, Applied Electrochemistry), and the carbon dioxide concentration by an infrared gas analyzer (BINOS-IR), both to an accuracy of 0.01%. We employed six channels simultaneously, using valves to switch between the channels once per minute (washout time 45 s), so that for each animal the values were recorded automatically at 6-min intervals. The system recorded the oxygen and carbon dioxide differentials between dried reference air and dried air from the metabolic box.

We calculated oxygen consumption and carbon dioxide production ($L \cdot h^{-1}$) using Eqn 6 of (15), in which the gas data are corrected for changes in gas volume resulting from the carbon dioxide production with the use of the respiratory quotient (RQ). The obtained values were converted to energy expenditure (kJ) by applying an energy equivalent of 20.1 $kJ \cdot L^{-1}$ O_2 (13). We calculated the average energy expenditure over the last 24 h of the measurement (daily energy expenditure (DEE)) as well as over the light (energy expenditure during the light (EEL)) and dark phases of the photoperiod (energy expenditure during the dark (EED)). Resting metabolic rate (RMR) was calculated as the lowest value of a 30-min running mean over the last 24 h of the measurement.

Body Composition

At the end of the experiment (at Day 190), the total body water volume (TBW) was determined by ^{18}O dilution (28). Six hours before light offset (0930-hours MET), food was removed. Three hours later, the animals were injected intraperitoneally with approximately 0.5 mL of $H_2{}^{18}O$ (91.37 atom %), sufficient to raise the ^{18}O concentration in the body water to 450 parts per million (ppm) excess. The amount of mixture injected was determined by weighing the syringe before and after injection to the nearest 1×10^{-4} g on an analytical balance (Mettler H54, Tiel, The Netherlands). After injection, the rats were returned to their home cages during a period of 1 h to allow for complete equilibration of the injected isotopes with body water. During this interval the animals were not allowed to drink or eat. After 1 h, we anaesthetized the animals lightly with CO_2, cut off 4 mm from the end of the tail, and collected blood in several 25 μL micropipettes, which were flame-sealed immediately. The animals were weighed before taking blood samples.

The isotopic enrichments of the blood samples were determined at the Center of Isotopic Research, University of Groningen, by means of isotopic ratio mass spectrometry (IRMS) and corrected for natural isotopic abundance (background) in body water. TBW (g) was estimated from the dilution space of ^{18}O:

$$\mathrm{TBW} = \frac{d}{\mathrm{MW}} \times 18.02 \times \frac{(F_d - F_a)}{(F_a - F_b)}$$

where d is the dose of $H_2{}^{18}O$ in grams, MW is the molecular weight of $H_2{}^{18}O$, and F_d, F_a, and F_b are the fractions of ^{18}O in the dose and in the blood samples after (F_a) and before (F_b) isotope administration, respectively. We calculated the lean body mass (LBM) (g) from the TBW values by assuming that the dilution space of ^{18}O overestimates TBW by 1% (28) and that 73% of the LBM consists of water (19); LBM = (TBW/10.1) × (1/0.73) g. Fat mass (FM in grams) was then calculated as the difference between body mass and LBM.

Data Analysis

Differences between group means were analyzed by Student's t test (SPSS Inc., 1988). The MANOVA (multivariate analysis of variance) procedure was used to test for the effects of photoperiod on gross energy intake and energy expenditure after correction for body mass. The repeated-measures procedure was used to test for the effect of photoperiod on growth rate, food intake, and growth efficiency to correct for the dependence of the consecutive measurements on the same animals. All tests were two-tailed, and significance was accepted at $p < 0.05$.

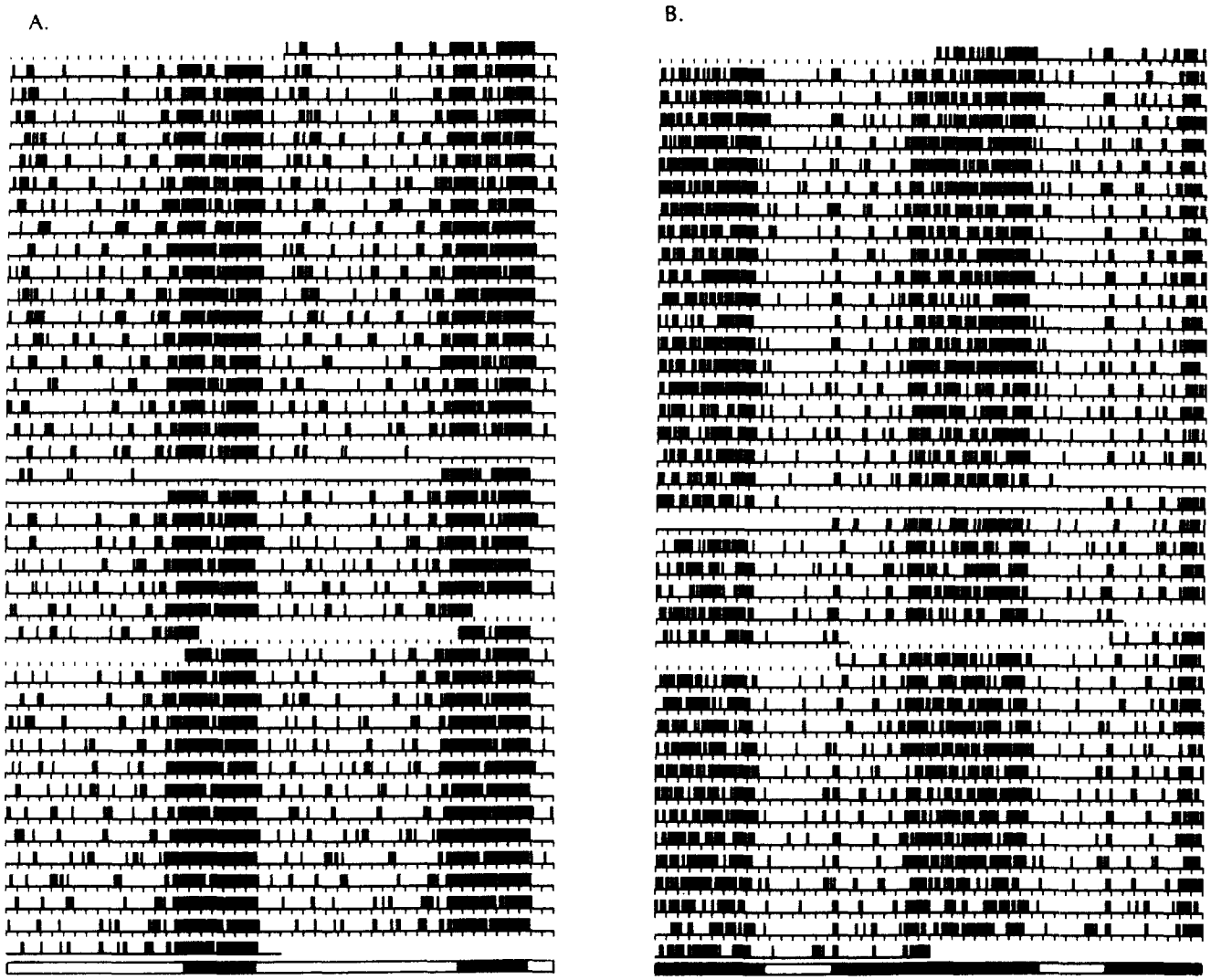

FIG. 1. Two representative double-plotted actograms of rats subjected to either a long (LD 18:6; A) or short photoperiod (LD 6:18; B).

RESULTS

Locomotor Activity

The activity pattern of both groups was highly synchronized with the light–dark cycle (Fig. 1). Most of the activity occurred during the dark, and only incidental bouts of activity were visible during the light phase. Animals subjected to a short photoperiod showed a short bout of activity at the onset of the night. This burst was followed by a 5–6-h episode in which activity was low or absent. Thereafter, a 10–12-h activity bout was visible until about 1 h before lights-on. The animals exposed to long days were highly active during the whole night. The start of daily activity occurred about 1–2 h before lights-off and lasted until the end of the night.

The total amount of activity, calculated as the sum of all movements over 24 h, did not differ between the two photoperiods, 6015 ± 1287 movements·day^{-1} for the long-photoperiod group and 7110 ± 647 movements·day^{-1} for the short-photoperiod group ($T(12) = 2.01$). The distribution of the activity was affected by photoperiod. Rats subjected to long days showed significantly more activity during the light episode, 2629 ± 605 movements·day^{-1} as opposed to 610 ± 145 movements·day^{-1} for the short-photoperiod group ($T(6,69) = -8.58$, $p < 0.001$), and significantly less activity during the night, 3386 ± 840 and 6501 ± 635 movements·day^{-1}, respectively ($T(12) = 7.83$, $p < 0.001$). The mean level of activity during the light episode was significantly different for the two photoperiods, 146 ± 34 movements·h^{-1} for the long-day group and 102 ± 24 movements·h^{-1} for the short-day group ($T(12) = -2.83$, $p < 0.05$). During the night, the activity level was also significantly higher in animals exposed to a long photoperiod, 564 ± 140 and 361 ± 35 movements·h^{-1}, respectively ($T(12) = -3.72$, $p < 0.01$).

Weight Gain

At the beginning of the experiment, body mass did not differ between the two experimental groups (Fig. 2A). Body mass reached at Day 190 was significantly different: 587.6 ± 52.1 g in the long-photoperiod group vs. 525.3 ± 32.3 g in the short-photoperiod group ($T(13) = 2.73$, $p < 0.05$). The mean rate of

body mass increase over the total experiment was significantly higher in rats subjected to long days (2.6 ± 0.2 g·day^{-1}) versus those subjected to short days (2.3 ± 0.2 g·day^{-1}) ($T(13) = 2.80$, $p < 0.05$). Growth rate (g·day^{-1}), calculated over 10-day periods, as a function of age is plotted in Fig. 2B. Growth rate over the first 80 days of the experiment was significantly higher in the long-photoperiod group (4.6 ± 0.4 g·day^{-1}) as opposed to the short-photoperiod group (4.1 ± 0.3 g·day^{-1}) ($F(1, 13) = 7.09$, $p < 0.05$). No difference in growth rate was visible over the last 110 days of the experiment, 1.2 ± 0.2 and 1.0 ± 0.2 g·day^{-1}, respectively ($F(1, 13) = 2.81$).

Gross Energy Intake

The gross energy intake (GEI), calculated as the mean intake over 10-day periods, is plotted as a function of age in Fig. 3A. No difference in the mean GEI during both the first 80 days and the last 110 days could be observed between the two groups ($F(1, 13) = 2.43$ and $F(1, 13) = 0.18$, respectively). The mean GEI over the whole experimental period was not dependent on photoperiod, 379.8 ± 25.5 and 367.2 ± 14.6 kJ·day^{-1}, respectively ($T(13) = -1.15$). Correcting GEI for body mass, by incorporating body mass as a covariate in the MANOVA analyses, did not show an effect of photoperiod on GEI ($F(1, 11) = 0.88$).

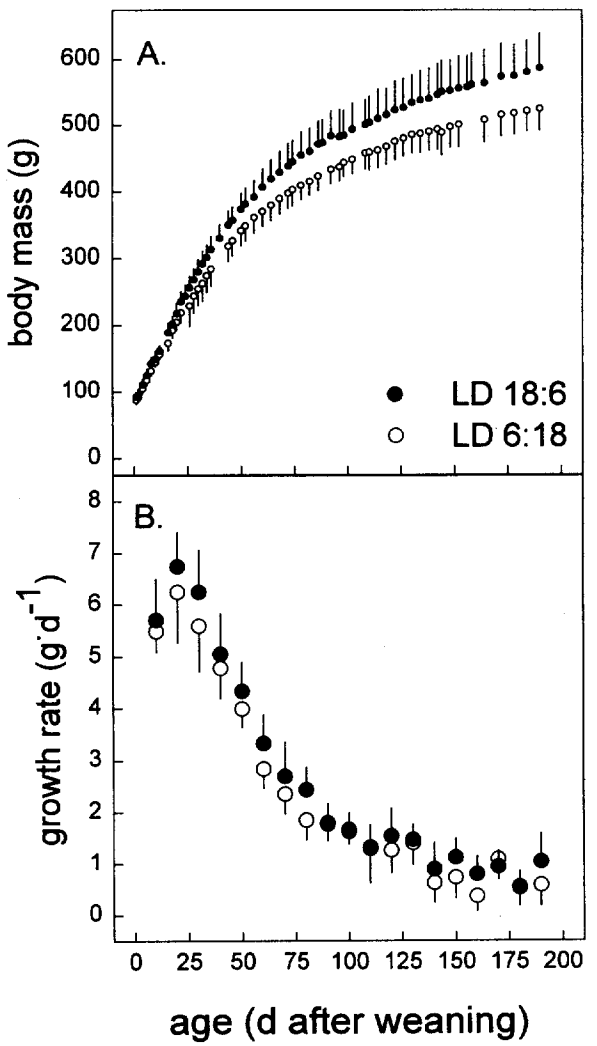

FIG. 2. (A) Body mass (g) and (B) growth rate (g·day^{-1}), calculated over 10-day periods, as a function of age in rats subjected to either a long (LD 18:6) or short photoperiod (LD 6:18). Values are means, and bars indicate SDs.

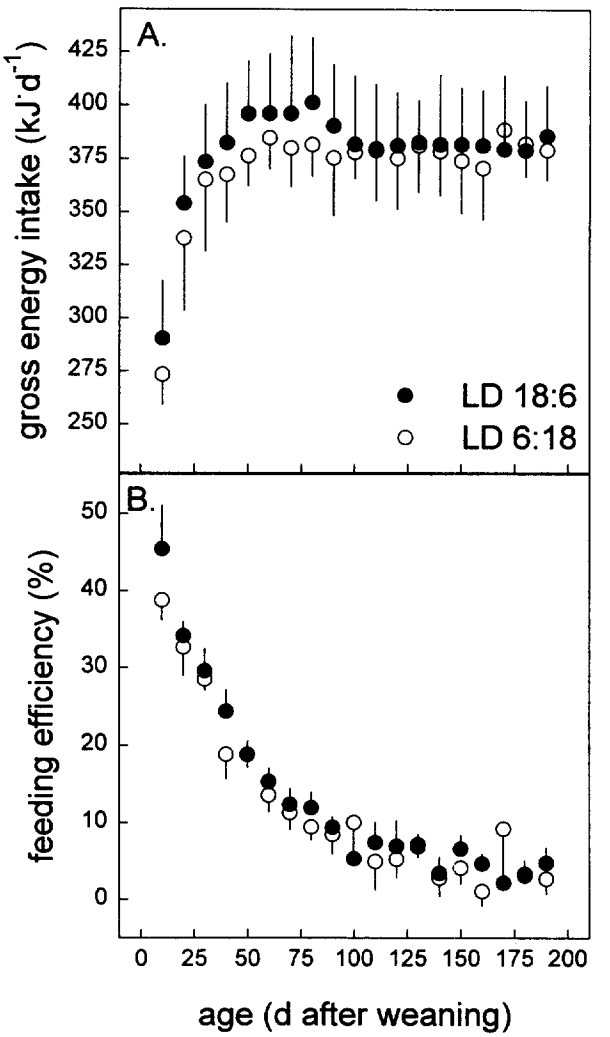

FIG. 3. (A) Gross energy intake (kJ·day^{-1}) and (B) growth efficiency (%) calculated over 10-day periods in relation to age in rats subjected to either a long (LD 18:6) or short photoperiod (LD 6:18). Values are means, and bars indicate SDs.

The distribution of energy intake over the 24-h period was significantly different for the two photoperiods. Rats subjected to long days consumed 46.1 ± 5.6% of their daily amount of energy during the light episode, as opposed to only 1.5 ± 2.6% for those subjected to short days ($T(13) = 20.08$, $p < 0.001$).

The mean growth efficiency over 10-day periods decreased as the animals increased their body mass and became stable around day 100 (Fig. 3B). The efficiency over the first 80 days was significantly higher in the group subjected to long days (23.4 ± 1.5%) versus that for the short-day group (21.4 ± 1.9%) ($F(1, 13) = 46.4$, $p < 0.001$). No difference occurred during the last 110 days of the experiment, 5.8 ± 0.6% and 5.0 ± 1.0%, respectively ($F(1, 13) = 0.29$) The mean efficiency over the total experimental period was significantly higher in the rats subjected to long days,

14.2 ± 1.1% and 12.6 ± 1.6%, respectively ($T(13) = -2.19, p < 0.05$).

Energy Expenditure

In Fig. 4A,B daily energy expenditure (DEE), resting metabolic rate (RMR), and energy expenditure during the dark (EED) and light (EEL) phases are plotted against age. Both DEE ($F(1, 67) = 6.5, p < 0.05$) and RMR ($F(1, 67) = 14.8, p < 0.01$) were affected by photoperiod after incorporation of body mass as a covariate in the MANOVA analyses, with higher rates in the group subjected to long days (Fig. 4A). Photoperiod, after correction for body mass also significantly influenced EEL ($F(1, 67) = 28.4, p < 0.01$) and EED ($F(1, 67) = 67.3, p < 0.01$) (Fig. 4B). For none of the energy variables was the interaction between experimental condition and body mass significant.

To examine if the effect of photoperiod on DEE could be attributed to the effect found on RMR, we incorporated RMR as a covariate in the MANOVA analyses for DEE and found that the effect of photoperiod on DEE disappeared ($F(1, 66) = 1.8, p > 0.05$).

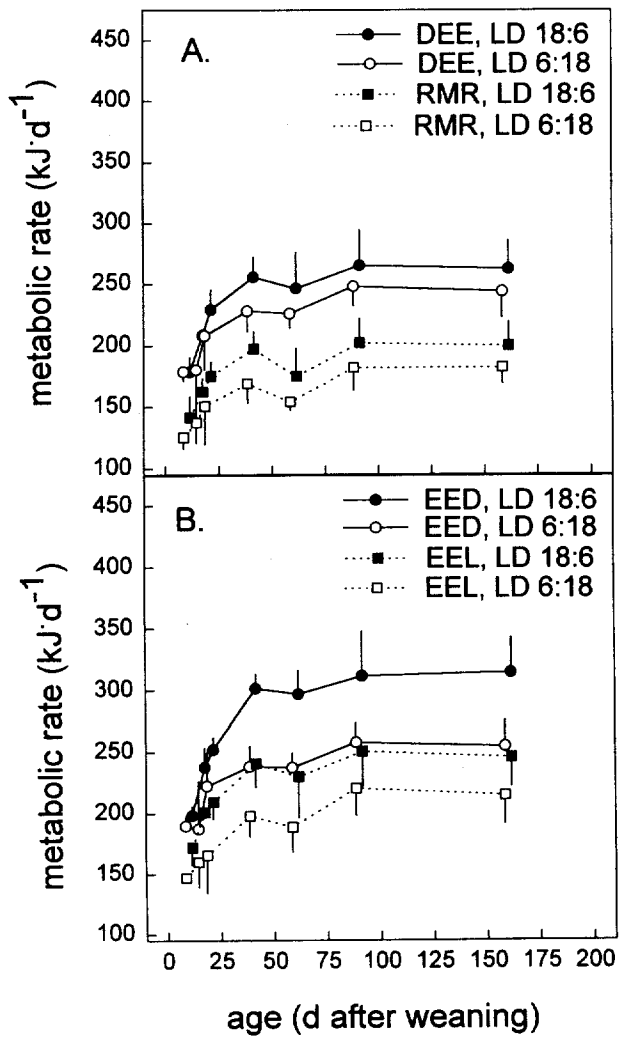

FIG. 4. Relationship between metabolic rate (A) daily energy expenditure (DEE) and resting metabolic rate (RMR); (B) energy expenditure during the dark (EED) and during the light phase (EEL) and age in rats subjected to either a long (LD 18:6) or short photoperiod (LD 6:18). Values are means, and bars indicate SDs.

TABLE 1

BODY COMPOSITION* (MEAN ± SD) AT 190-DAYS AFTER WEANING IN RATS EXPOSED EITHER TO A LONG (LD 18:6) OR SHORT PHOTOPERIOD (LD 6:18)

	LD 18:6 (n = 8)	LD 6:18 (n = 7)
BM†		
g	581 ± 49	525 ± 34
TBW		
g	346 ± 16‡	323 ± 23
%	60 ± 3	61 ± 1
FM		
g	107 ± 33	81 ± 12
%	18 ± 4	15 ± 2
LWM		
g	474 ± 21‡	445 ± 31
%	82 ± 4	85 ± 2

* Based on the dilution space of ^{18}O. For more details, see method section.

† BM: body mass; TBW: total body water; FM: fat mass; LWM: lean wet mass.

‡ $p < 0.05$.

Body Composition

Based on the dilution space of ^{18}O, the total body water volume (TBW) of both groups of animals was estimated, and FM and LBM were calculated. The values are listed in Table 1. LBM and TBW were significantly affected by photoperiod ($T(13) = 2.18$, $p < 0.05$ and $T(13) = 2.27$, $p < 0.005$, respectively), with higher values in the group subjected to a long photoperiod. FM and percentage of water, fat, and lean mass did not differ significantly between the two photoperiods.

DISCUSSION

This experiment shows that the rat, which is a nonseasonal breeder and usually not considered to be responsive to day length (7,34), is sensitive to photoperiod during early development. Juvenile Wistar rats exposed to short photoperiods (a) have a lower growth rate, (b) have similar energy intake, (c) have lower growth efficiency, (d) have lower DEE and RMR, and (e) gain less lean body mass than those exposed to long photoperiods. It was also shown that rats exposed to either a long or short photoperiod have no difficulty synchronizing their activity pattern to an extreme light–dark cycle.

Extensive studies have shown seasonal cycles of body mass in voles and hamsters that are regulated by photoperiod (2,5,6,8–10,20,33). The reproductive system of these animals is also responsive to day length (1,5,6,8), so that changes in hormone levels can in part be responsible for the observed changes in body mass (7,34). Other factors that play a role in determining the effect of photoperiod on body mass in these species are changes in food intake (3,9,11,12) and changes in energy efficiency (3). Growth in lean Zucker rats is not responsive to photoperiod, whereas obese Zucker rats do react with higher body masses when subjected to a long photoperiod (17). It was hypothesized (17) that this effect was caused by a reduction in energy expenditure (extension of the

resting phase) and/or by a positive effect of photoperiod on metabolic efficiency by forcing the animals to consume the same amount of energy in a shorter time period. The results of our study did not confirm these hypotheses. In growing rats, an extension of the resting phase (light) resulted in an increase in daily energy expenditure, and not a reduction. We did observe a higher growth efficiency in rats subjected to long days, as hypothesized in (17). However, we cannot conclude from our data that this was caused by a limitation of the feeding time. Rats subjected to a dark period of only 6 h per day learn to consume almost 50% of their daily energy intake during the light period.

The effect of photoperiod on daily energy expenditure was explained by a difference in RMR between the two groups. We calculated RMR as the lowest value of a 30-min running mean over the last 24 h of the energy measurement. This value is dependent on activity level. Although we showed that the total amount of activity did not differ between the two groups, the distribution did. Rats in the long-photoperiod group had a higher level of activity and showed more regular bouts of activity during the light phase than rats subjected to short days, which may have prevented energy expenditure from reaching low values. Another possible explanation for higher RMR values in the long-photoperiod group is feeding condition. We showed that rats subjected to long days learn to consume almost 50% of their daily energy intake during the day, while the short-photoperiod group consumes its energy mainly during the night. Although we are not able to say something about the distribution of food intake over the light period (if the animals fast for a couple of hours directly after lights-on or nibble along during the whole light episode), it is possible that during this period the long-photoperiod animals were in a relatively constant feeding condition. They could therefore not reduce their energy expenditure as much as the other group during the light phase and had consequently higher RMR values. Rats that are only fed two meals a day have a lower maintenance energy level than rats that are allowed to eat ad lib. (29). The higher values found for EED (energy expenditure during the dark phase) in the long-photoperiod group were caused by a higher level of activity exhibited by this group during both phases relative to rats exposed to short days. The difference in energy expenditure between the light and dark phases of the photoperiod was larger in the long-photoperiod group than in the short-photoperiod group (Fig. 4B), probably because of the factors mentioned earlier (feeding condition, activity pattern). Possibly, these fluctuations in energy expenditure over the day had an effect on total energy balance.

The possible difference in food intake pattern, apart from having an effect on the distribution of energy expenditure over the photoperiod, could also have influenced growth efficiency. Eating the same amount of energy broadly distributed over 24 h as opposed to a restricted period during the night might have led to differences in growth efficiency. Studies in both rats and humans in which the effect of "nibbling" (ad lib. food intake) and meal feeding (2–4 meals per day) was investigated on growth efficiency have shown no clear effect of feeding pattern (4,23,30,35). However, these studies examined the effect of feeding frequency on growth efficiency in conditions of weight gain after a period of weight loss (4,35), or in combination with different diets (23), and are therefore not directly comparable with our study. Although rats in the short photoperiod did not eat during the light phase, they still had 18 h during the night for feeding. The long-photoperiod group distributed its food intake over the whole 24 h but still ate at the highest rate during the night phase (same amount of energy in 6 h as in 18 h). This situation is not directly comparable with meal feeding and "nibbling", and therefore an effect of feeding pattern on growth efficiency in our study cannot be excluded.

Another effect found of photoperiod in this study is the effect on body composition. Rats subjected to long days gained significantly more lean body mass than animals subjected to short days. When expressed as a percentage of total body mass, there was no difference. It was previously found (17) that obese Zucker rats exposed to a long photoperiod had a higher lean body mass, and this was attributed to possible altered testosterone levels in the obese Zucker rat.

Rats subjected to a long photoperiod from weaning had a higher growth rate relative to rats subjected to a short photoperiod, despite higher energy expenditure levels shown by the first group and the absence of differences in food intake. Growth efficiency was higher in the long-photoperiod group, but it is unlikely that this difference in efficiency accounts for the difference in growth rate between the two photoperiod groups. It seems that the effect of photoperiod on growth in rats is generated by small effects on food intake, growth efficiency, and energy expenditure that accumulate over time and result in differences in body mass gain. The difference in growth rate described here was about 0.4 $g \cdot day^{-1}$ during the first 80 days. If we presume that 1 g of weight increase in young rats consists for 20% of fat and 13% of protein (26), that the synthesis costs of 1 g of fat and 1 g of protein are 39.5 and 23.6 kJ, respectively, and that the efficiency of biosynthesis is 75% (25), the daily difference in energy balance between the two different photoperiods would be about 7.5 $kJ \cdot day^{-1}$. This is a marginal difference which will be difficult to verify, but which did, by a cumulative effect, lead to a difference in body mass over time.

In conclusion, the effect of photoperiod on growth in rats is clear, in spite of small differences in growth rate on a daily basis. These differences in body mass gain are most likely produced by differences in the distribution of energy expenditure, and possibly food intake, over the 24-h cycle.

ACKNOWLEDGEMENTS

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